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Effects of moderate feed restriction on energy expenditure by 2-year-old crossbred Boer goats

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Abstract

Fourteen Boer (75%) \times Spanish wether goats (51 \pm 1.8 kg BW and 23 months of age) were used to determine effects of a moderate degree of nutrient restriction on heat production or energy expenditure (EE). The experiment consisted of a 26-day period (P1) followed by one of 50 days (P2). Wethers were fasted on the final 4 days of each period, with gas exchange measured on the last 2 days. Fasting was preceded by collection of feces and urine for 7 days, with the final 2 days for gas exchange. All wethers were fed a 65% concentrate diet at a level of intake near maintenance in P1 (P1-100 and P1-80 treatments). In P2, six wethers continued on this level of intake (P2-100 treatment); eight wethers also were fed at this level for 15 days but then had ME intake sequentially reduced by approximately 10 and 20% for 10 and 21 days, respectively (P2-80 treatment). This schedule was chosen because of a similar one used in a separate experiment to compare different goat genotypes and diet nutritive values. Intake of ME was lowest (P < 0.05) for P2-80 (529, 535, 552, and $474 \text{ kJ/kg BW}^{0.75}$ (fasted) for P1-100, P1-80, P2-100, and P2-80, respectively). Fed EE was lowest (P < 0.05) for P2-80 $(495, 505, 467, and 406 \, kJ/kg \, BW^{0.75})$, whereas EE while fasting was similar among treatments $(287, 279, 273, and 253 \, kJ/kg \, BW^{0.75})$ for P1-100, P1-80, P2-100, and P2-80, respectively). The ME requirement for maintenance (ME_m) was greater (P < 0.05) in P1 than P2 (477, 487, 421, and 376 kJ/kg BW^{0.75} for P1-100, P1-80, P2-100, and P2-80, respectively), and when P2 data were analyzed separately ME_m was lower (P < 0.10; 374 kJ/kg BW^{0.75} versus 425 kJ/kg BW^{0.75}) and the efficiency of ME use for maintenance was greater (P < 0.08) for P2-80 than for P2-100 (0.689 versus 0.625). In conclusion, moderate feed intake restriction impacted EE and ME_m by mature meat goats largely via decreasing EE that is responsive to nutrient intake rather than EE of basal metabolism when fasting. © 2006 Elsevier B.V. All rights reserved.

Keywords: Goats; Energy; Feed intake

1. Introduction

Goats are able to thrive in a variety of environments, many of which entail periods of low nutrient intake.

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Low nutritional planes reduce heat production or energy expenditure (EE) by cattle and sheep (Freetly et al., 2002, 2003). Reduced EE has also been observed in desert goats with severe feed restriction (Silanikove, 1986, 1987; Choshniak et al., 1995). However, effects of moderate feed intake restrictions on energy utilization by goats typical of many other production systems have not been extensively investigated.

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Boer and Boer crossbred goats have become quite popular for meat goat production in the U.S. The relatively high growth rate of Boer crossbreds compared with other meat goats with moderate to high nutritional planes has been well established (Huston and Waldron, 1996; Roeder et al., 1997; Prieto et al., 2000; Negesse et al., 2001; Urge et al., 2004). With a compiled database of treatment mean observations from the literature, Luo et al. (2004b) determined that the maintenance energy requirement of goats with 50% or more Boer breeding is similar to that of indigenous or local goats, such as the Spanish of the U.S. However, most observations were with BW change near or above zero and, thus, how maintenance energy requirements might change after BW loss is unknown. Joemat et al. (2004) suggested that a constant and moderate plane of nutrition compared with a fluctuating level is more important for continual growth and development of yearling crossbred Boer doelings compared with Spanish, implying limited change in EE of Boer crossbreds with varying nutritional plane. But, in Joemat et al.'s (2004) study a low quality forage was consumed ad libitum and periods of nutrient restriction appeared to entail limited absorption of both energy and nitrogen rather than of energy alone.

Objectives of this experiment were to determine effects on energy utilization by 2-year-old crossbred Boer goats of a moderate restriction of feed intake, as well as to assess the relative importance of different contributing physiological processes.

2. Materials and methods

2.1. Animals, diet, and treatments

Fourteen 3/4 Boer \times Spanish wether goats, 23 \pm 0.5 months of age and 51 ± 1.8 kg BW, were used. Wethers were treated for internal parasites (Valbazen, SmithKline Beecham Animal Health, West Chester, PA) at the beginning of the experiment and were housed in a facility with temperature controlled at 20-23 °C. A concentrate-based diet (Table 1) was fed based on an assumed ME requirement for maintenance (ME_m) of 438 kJ/kg BW^{0.75} (AFRC, 1998), initial BW, and a dietary concentration of 11.3 MJ/kg DM as determined from ingredient proportions and ME concentrations of NRC (1981). The experiment was divided into two periods, the first 26 days in length and the second 50 days. Periods consisted of three segments: adaptation (15 days for period 1 and total of 39 days for period 2), nutrient balance determination (7 days), and fasting (4 days). During nutrient balance segments and the last 2 days of fasting, wethers resided in metabolism crates. Housing at other times was in $1.05 \,\mathrm{m} \times 0.55 \,\mathrm{m}$ elevated pens with plastic-coated expanded metal floors.

In the first period, all goats were fed the diet to supply 100% of maintenance for 22 days. In the second period, six goats

Table 1 Composition of the diet fed to Boer × Spanish wethers

Item	DM (%)
Ingredient	
Ground alfalfa hay	35.00
Ground corn	55.50
Soybean meal	3.50
Molasses	3.00
Dicalcium phosphate	0.72
Limestone	0.28
Vitamin premix ^a	0.50
Trace mineralized saltb	0.50
Ammonium chloride	0.50
Sodium sulfate	0.50
Chemical composition	
Ash	6.1
CP	13.5
NDF	24.0
ADF	18.7
Acid detergent lignin	4.6

 $[^]a$ Contained 2200 IU/g Vitamin A, 1200 IU/g Vitamin D₃, and 2.2 IU/g Vitamin E.

remained at this level of feeding. The other eight wethers also continued at this level for 15 days but then were sequentially changed to ME intake levels of approximately 90 and 80% of maintenance for 10 and 21 days, respectively. This regime was similar to that used in a separate, independent study at the Institute to compare different goat genotypes and diet nutritive values (Tovar-Luna et al., in press). Feed was offered in equal amounts twice daily at 08:00 and 15:00 h. Water was offered in buckets twice daily at 10:00 and 16:30 h for 3 min periods. Wethers were weighed at the beginning of the experiment, at changes in level of feed intake, and at the beginning and end of nutrient balance and gas exchange measurement times.

2.2. Nutrient balance

During nutrient balance segments, feed offered, feed refusals or orts, feces, and urine were recorded with an accuracy of 1 g (Cochran and Galyean, 1994). As noted later, there were some instances in which feed refusals were relatively large, resulting in data omission from analyses. Also, in period 1 there were some small feed refusals for other animals. Feces were collected in wire-screen baskets placed under the floor of the crates, and urine was collected through a funnel into plastic buckets containing 10 ml of a 10% (v/v) solution of sulfuric acid. 15% aliquots of daily excretion of urine and feces were collected and stored at $-20\,^{\circ}\mathrm{C}$ until later analyses.

Feed, orts, and feces were first dried in a forced air oven at 55 °C for 48 h then ground to pass a 1 mm screen. Thereafter, composite samples were formed for each animal and period. Feed samples were analyzed for DM, ash, N, gross energy

^b Contained 95–98% NaCl and at least 0.24% Mn, 0.24% Fe, 0.05% Mg, 0.032% Cu, 0.011% Co, 0.007% I, and 0.005% Zn.

(GE; AOAC, 1990), NDF, ADF, and ADL (filter bag technique; ANKOM Technology Corp., Fairport, NY), and fecal samples were analyzed for DM, ash, GE, N, and NDF. Urine samples were assayed for DM (lyophilization), and N and GE concentrations were determined with lyophilized samples.

2.3. Gas exchange

For gas exchange measures, wethers were assigned to different sets consisting of four animals, with the start of measures for the sets staggered by 2 days. Prior to measures, wethers had been placed in metabolism crates fitted with training head boxes for adaptation. Air exchange in the calorimetry room (6 m width, 7 m length, 2.8 m height) was controlled by an exhaust fan (1300 l/m; Broan, Hartford, CT), mounted on a wall in juxtaposition to the ceiling, with an air inlet port located in the ceiling of the opposite corner of the room. The calorimetry room was well sealed from adjacent equipment and animal rooms. To achieve uniform gas concentrations throughout the calorimetry room, a rotating ceiling fan (2.5 m height) was situated in the middle of the room. Temperature (20-23 °C) in the calorimetry room was maintained with a window air conditioning/heating unit (Carrier; Farmington, CT), and humidity was 50-55% through use of a dehumidifier (Whirlpool; Benton Harbor, MI). Natural photoperiod was mimicked by use of fluorescent lights.

Oxygen consumption and production of carbon dioxide and methane were measured with an open circuit respiration calorimetry system (Sable Systems, Las Vegas, NV) with four Lexan® (General Electric, New York, NY) head boxes (41 cm width, 27 cm depth, 92 cm height) fitted in four metabolism crates (46 cm width, 46 cm depth, 158 cm height) placed in a calorimetry room the last 2 days of nutrient balance and fasting segments. Head boxes included a removable drawer for feeding and watering (23 cm height in the front, 15 cm height in the back (closest to animal), 40 cm wide, 28 cm depth). The head opening was 30.5 cm wide and 55 cm high beginning at the top of the drawer. A 'sock' of Cordura® nylon (DuPont, Wilimington, DE) attached to the opening of the head box fitted with a 25 cm long zipper was held snug to the neck of the wether with Velcro® (Velcro USA Inc., Manchester, NH) and ElastikonTM (Johnson & Johnson, New Brunswick, NJ) ties. In addition, ElastikonTM ties were used to prevent looseness in the sock to avoid chewing of the material. There was a small fan situated at the top of the head box used to mix air and a 7 cm i.d. hose to transport air from the head box to the mass controller and pump (50–150 l/min; Flowkit500, Sable Systems). Flow rate (50-150 l/min) for each station was set to achieve minimum differences between air inflow to and outflow from the head box of 0.2% O₂ and CO₂. A smaller pump (0.5 ml/min; Thomas 8003, Puchheim, Germany) was used to sub-sample air from the main pump. Air from head boxes and the room was delivered sequentially to a dew point analyzer, drying filter, multiplexer, and gas analyzers. A 0.5 cm i.d. tube was placed in the center of the room for sampling of reference air.

Oxygen concentration was analyzed using a fuel cell FC-1B oxygen analyzer (Sable Systems). Carbon dioxide and methane

concentrations were measured using infrared analyzers (FC-1B for CO₂ and MA-1 for CH₄; Sable Systems). Air was first analyzed for CH₄ then for CO₂ and O₂. With four stations employed, concentrations of gases in air from each station were analyzed six times per hour (14 min interval when reference air was sampled and 8 min interval when only the four stations were sampled). Dwell time for reference air was set at 3 min, recalibration to head box air was for 3 min, and time for sampling of station air was 2 min. Reference air was sampled twice per hour. Collected data consisted of the average of the last five measurements in each cycle of the three gas analyzers, temperature, and humidity, along with dewpoint and air flow rate through head boxes, all recorded on a PC using software of Sable Systems. Prior to gas exchange measurements and approximately every 6 weeks thereafter, validity and accuracy of expired CO2 and inspired O2 flows were checked by reference to alcohol combustion (average 101.3 ± 1.1 and $100.3 \pm 1.6\%$ of expected CO₂ production and O₂ consumption, respectively). Before each test analyzers were calibrated with reference gas mixtures (19.5 and 20.5% O2, 0.0 and 1.5% CO₂, and 0.0 and 0.3% CH₄).

2.4. Calculations

ME intake was calculated from GE intake and feces, urine, and methane losses. EE was estimated based on Brouwer (1965) equation. In addition to use of oxygen consumption and carbon dioxide and methane production, urinary N excretion determined during both the nutrient balance and fasting segments was employed. EE and ME intake were expressed relative to average BW within the 2-day period of determining fasting EE. Efficiency of utilization of ME for maintenance $(k_{\rm m})$ was estimated by regressing the difference between ME intake and EE against ME intake, with ME_m determined by dividing fasting EE by $k_{\rm m}$.

2.5. Statistical analyses

Data were first analyzed by mixed model analysis (Littell et al., 1996), with a repeated measure of period and random effect of animal. In addition, dietary treatments in period 2 were compared via general linear models procedures of SAS (1998), as a completely randomized design using period 1 data as covariates (Steel and Torrie, 1980). In order to avoid tabular redundancy, the separate analysis of period 2 data was addressed by inclusion in Table 2 of the *P*-value for the difference between dietary treatments. However, because of covariate usage, there were differences in means and SE between methods, albeit small, which are addressed in the text.

3. Results

Four observations from three wethers were omitted because of low feed intake ($64 \pm 12\%$ of that offered) on days when gas exchange was measured. Therefore, all data for the one animal with poor consumption in

Table 2 Effects of feed intake restriction on energy utilization by 2-year-old Boer \times Spanish wethers

Item	Period 1 ^a				Period 2 ^a			Effect ^b (<i>P</i> <)				
	100	S.E.	80	S.E.	100	S.E.	80	S.E.	T	P	$T \times P$	LIP2
n	6		7		4		7					
BW (kg)												
Initial	51.3	2.79	51.9	2.58								
Fed ^c	45.2	2.21	46.2	2.04	46.9	2.70	43.6	2.04	0.60	0.83	0.34	0.01
Fasted ^d	42.8	2.21	43.2	2.05	45.2	2.71	41.1	2.05	0.42	0.94	0.34	0.03
Digestion (%)												
DM	74.5	1.37	75.8	1.27	76.6	1.67	79.8	1.27	0.13	0.04	0.51	0.04
OM	76.4	1.29	77.5	1.19	78.7	1.57	82.3	1.19	0.09	0.01	0.35	0.03
CP	72.3	1.83	74.7	1.69	73.4	2.24	78.4	1.69	0.06	0.21	0.48	0.03
NDF	74.0 a	0.89	74.3 a	0.83	75.2 a	1.09	81.7 b	0.83	0.01	0.01	0.01	0.01
Energy	77.4 ab	0.94	76.6 a	0.87	75.8 a	1.09	79.8 b	0.87	0.11	0.42	0.02	0.04
Intake												
DM (g/day)	702 b	26.2	716b	24.3	773 b	32.1	582 a	24.3	0.01	0.26	0.01	0.01
N (g/day)	14.90 b	0.557	15.39 bc	0.516	16.70 c	0.682	12.55 a	0.516	0.01	0.38	0.01	0.01
GE (MJ/day)	12.98 b	0.484	13.22 b	0.448	14.25 b	0.593	10.72 a	0.448	0.01	0.23	0.01	0.01
DE (MJ/day)	10.04 b	0.337	10.11 b	0.312	10.78 b	0.413	8.57 a	0.312	0.01	0.26	0.01	0.01
ME (MJ/day)	8.83 b	0.336	8.98 b	0.311	9.60 b	0.412	7.68 a	0.311	0.01	0.46	0.01	0.01
ME ($kJ/kg BW^{0.75}$)	529 b	13.7	535 b	12.7	552 b	16.7	474 a	12.7	0.01	0.18	0.01	0.01
Energy (MJ/day)												
Feces	2.94 b	0.199	3.11 b	0.185	3.47 b	0.244	2.16 a	0.185	0.01	0.31	0.01	0.01
Urine	0.53	0.034	0.40	0.031	0.44	0.042	0.40	0.031	0.02	0.26	0.22	0.89
Methane	0.68 b	0.056	0.73 b	0.052	0.74 b	0.069	0.48 a	0.052	0.09	0.11	0.01	0.05
N (g/day)												
Feces	3.43 b	0.294	3.58 bc	0.273	4.46 c	0.361	2.65 a	0.273	0.01	0.88	0.01	0.01
Urine	4.65	0.762	3.85	0.706	3.80	0.933	5.12	0.706	0.74	0.79	0.19	0.42
Energy expenditure (kJ/k	(g BW ^{0.75})											
Fed	495 b	14.3	505 b	13.3	467 b	17.6	406 a	13.3	0.09	0.01	0.03	0.01
Fasted	287	11.4	279	10.5	273	13.9	253	10.5	0.23	0.09	0.63	0.57
$\mathrm{ME_m}^{\mathrm{e}} \ (\mathrm{kJ/kg} \ \mathrm{BW}^{0.75})$	477	21.7	487	20.1	421	26.6	376	20.1	0.44	0.01	0.23	0.10
$k_{ m m}{}^{ m f}$	0.606	0.0215	0.577	0.0199	0.648	0.0263	0.676	0.0199	0.97	0.01	0.21	0.08

Interaction means in a row without common letters (a–c) differ (P<0.05).

^a Periods 1 and 2 were 26 and 50 days, respectively. All wethers (80 and 100 levels of intake) in period 1 were fed at a level of intake near maintenance. In period 2, 100 wethers were fed at a level of intake near maintenance, whereas 80 wethers were fed at this level for 15 days and then sequentially received feed to supply approximately 90 and 80% of previous ME intake in the subsequent 10 and 21 days, respectively.

^b T = dietary treatment, P = period, $T \times P$ = dietary treatment \times period interaction, and LIP2 = comparison of 100 and 80 levels of intake in period 2.

^c Average during the 2-day gas exchange measurement period in the fed state, which occurred near the end of the periods.

^d Average during the 2-day gas exchange measurement period in the fasted state, which occurred on the last 2 days of the periods.

^e ME requirement for maintenance.

f Efficiency of ME utilization for maintenance.

each period (80% of maintenance treatment) were omitted. Factors responsible for low intake by the other two wethers in period 2 (100% of maintenance treatment) are unclear. However, the longer period of confinement for period 2 versus period 1 measures may have been involved. Also, typically feed intake when animals are placed in metabolism crates is lower than when in small pens that allow greater movement.

Wethers on the 100 and 80% of maintenance treatments exhibited similar BW loss in period 1 from its beginning to nutrient balance and fasting segments and from the beginning to end of fasting (Table 2). However, as expected, BW loss from period 1 to 2 was greater for wethers on the 80 than 100% of maintenance treatment.

Lowest intakes among treatments (i.e., feed intake level and period combinations) for 80% of maintenance in period 2 corresponded to greatest (P < 0.05) digestibilities of NDF and energy (Table 2). Based on separate analyses of period 2 data, digestibilities of other dietary fractions were greater (P < 0.05) for 80% versus 100% of maintenance as well. Urinary energy excretion was greater (P < 0.05) for 100% versus 80% of maintenance wethers. Methane emission was lowest among treatments (P < 0.05) for 80% of maintenance in period 2.

Estimates of fasting EE and ME_m (Table 2) were in the range of values for goats summarized by AFRC (1998, fasting: 212–403 kJ/kg BW^{0.75}; ME_m: 365–530 kJ/kg BW^{0.75}), and fasting EE was not greatly different from that found by Luo et al. (2004a, 298 kJ/kg BW^{0.75}) by regressing retained energy against ME intake with a compiled database of treatment mean observations. EE when fed was lowest among treatments (P < 0.05) for 80% of maintenance in period 2, although fasting EE was not influenced by a dietary treatment x period interaction (P>0.10). ME_m tended (P<0.10) to be lower in period 2 for 80% versus 100% of maintenance when period 2 data were analyzed separately (374 kJ/kg BW^{0.75} versus 425 kJ/kg BW^{0.75}). In accordance, separate period 2 data analysis resulted in greater $k_{\rm m}$ for 80% versus 100% of maintenance (P < 0.08; 0.689 versus 0.625).

4. Discussion

4.1. Feed intake and digestion

As noted in the present experiment, feed intake level can affect nutrient digestibility (Tyrrell and Moe, 1975; Staples et al., 1984; Silanikove, 1992; Merchen and Bourquin, 1994), which appears associated with factors such as slower passage of digesta through the gastrointestinal tract (Van Soest, 1994) and(or) increased ratios of digestive/absoptive enzymes to substrates (McAllister et

al., 2001). Digestion of structural carbohydrates is most affected by level of intake compared with other dietary fractions (Tyrrell and Moe, 1975; Reid et al., 1980).

4.2. BW change

Decreased BW in period 1 may be partially attributable to decreased gastrointestinal tract digesta fill, which is supported by an average of 68% of the loss occurring in the first 11 days. Previously, wethers had grazed a grass based pasture with moderate-high forage mass. Furthermore, because of an underestimation of the dietary ME concentration, perhaps relating to the assumed level in corn, ME intake was slightly above that intended. This contributed to tissue energy accretion on the two gas exchange measurement days near the end of the period. As expected, BW of wethers on the 80% of maintenance treatment decreased from the balance segment of period 1 to that of period 2. However, in period 2, BW was similar before and after the nutrient balance period (43.7 kg versus 43.4 kg; S.E. = 1.75) and, again, ME intake was slightly greater than EE regardless of level of intake. In this regard, animals fed below assumed ME_m for extended periods of time eventually achieve BW equilibrium with reduced ME_m (Taylor and Young, 1968, Williams and Jenkins, 2003).

4.3. 100% of maintenance treatment

Actual ME_m may be slightly less and $k_{\rm m}$ greater than estimates of this study because of EE attributable to energy accretion and a lower efficiency of energy use for gain than for maintenance alone. However, change in heat increment relative to ME intake is gradual rather than abrupt (at the point at which EE equals ME intake) as intake increases. ME_m corrected for retained energy was not presented because efficiency of energy metabolism varies among individuals and the need to make assumptions of the efficiency of ME use for gain and energy concentration in accreted tissue. Also, energy retention did not differ among treatments. Nonetheless, because of energy retention, these ME_m and k_m estimates may have greatest value for within experiment treatment comparisons and should not be directly contrasted to findings of other studies without consideration of differences in experimental conditions.

Similar to ME_m in period 1, Luo et al. (2004b) determined a ME_m of growing meat goats of 489 kJ/kg $BW^{0.75}$, although Sahlu et al. (2004) proposed a 7.5% lower value for wethers and doelings. Insufficient data were available for Luo et al. (2004b) to directly determine a ME_m for mature meat goats. However, because

of a similar estimate for growing meat and indigenous goats, Sahlu et al. (2004) and Nsahlai et al. (2004) suggested that the ME_m determined for mature indigenous and dairy goats could be adjusted for the difference between growing meat and indigenous versus dairy goats to derive a ME_m of 423.1 kJ/kg BW^{0.75} for mature meat goats, which is not greatly different from that initially assumed (438 kJ/kg BW^{0.75}; AFRC, 1998). However, wethers in this experiment were approximately 2 years of age, and Luo et al. (2004a) classed growing goats as being less than 1.5 years of age and those older as mature. Decreases in ME_m of other ruminant species with increasing age are gradual rather than abrupt (Freetly et al., 2002, 2003). Hence, a more appropriate ME_m on which to have based ME intake in the present experiment could have been greater than that used, such as between 423 or 438 and $489 \,\mathrm{kJ/kg} \,\mathrm{BW}^{0.75}$.

4.4. 80% of maintenance treatment

EE by wethers subjected to the 20% feed restriction was 17% lower in period 2 than in period 1 and 12% less than for wethers fed at maintenance in period 2. Factors responsible for numerically lower EE and ME_m when fed for 100% of maintenance wethers in period 1 versus period 2 are unknown, but could involve decreased EE by peripheral skeletal muscle as time in confinement increased. Nonetheless, fasting EE did not significantly differ with period or level of intake, but numerically was 4% or 10 kJ/kg BW^{0.75} lower for 80% versus 100% of maintenance when period 2 data were analyzed separately. These results indicate that moderate degrees of feed intake restriction can have considerable impact on EE of crossbred Boer goats, imparted primarily through $k_{\rm m}$ or EE above that while fasting, with change in ME_m being approximately 65% of the restriction in ME intake. Therefore, the majority of change in EE seems attributable to organs and tissues that are responsive to nutrient intake, primarily splanchnic tissues (Johnson et al., 1990), rather than only to ones responsible for heat generation of basal metabolism while fasting. This suggests that level of feed intake before the restriction period and perhaps the physical nature of the diet (Goetsch, 1998), in addition to severity of the restriction, may impact the magnitude of change in EE in periods of limited nutrient intake. However, other factors making smaller adaptive contributions to restricted feed intake were increased digestibility, decreased methane loss, and numerically lower fasting EE.

Decreased mass of metabolically active visceral tissues when feed intake is restricted has been observed with other ruminant species and appears responsible for much of change in ME_m (Drouillard et al., 1991; Wester et al., 1995; Sainz and Bentley, 1997), as is implied by findings of the present study. However, it is likely that with very limited feed intake there is involvement of other tissues (Silanikove, 1986, 1987, 2000a,b). In support, Choshniak et al. (1995) suggested that decreased oxygen consumption by desert goats in metabolism crates with severely restricted feed intake was not related to splanchnic tissue metabolism but rather to decreased oxygen use by other tissues, particularly peripheral skeletal muscle. But, movement on a treadmill increased oxygen consumption to the same level as for goats fed free-choice, although speed was rapid. Also, tissue distribution of blood flow, used to determine contributions of organs and tissues to reduced oxygen consumption by restricted goats, was performed in the morning well before the one daily meal after which whole body oxygen consumption increased to a relatively greater extent for restricted than for free choice-fed goats.

5. Summary and conclusions

Two-year-old crossbred wethers adapted to a 15–20% reduction in ME intake from a level near that for maintenance primarily by decreasing heat production above that while fasting. This suggests appreciable change in metabolism by tissues highly influenced by nutrient absorption, notably the gastrointestinal tract and liver. However, other factors made small contributions that facilitated a small degree of energy accretion not significantly different from that with the higher level of intake, which include a slight increase in digestion, decreased methane emission, and numerically decreased fasting heat production. Further research should consider other limited nutrient intake scenarios such as ad libitum consumption of low quality forage and different supplement treatments that might influence change in metabolism by the digestive tract and liver.

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References

AFRC, 1998. The Nutrition of Goats. CAB International, Oxon, UK, pp. 41–51.

AOAC, 1990. Official Methods of Analysis, 15th ed. Association of Official Analytical Chemists, Washington, DC.

Brouwer, E., 1965. Report of sub-committee on constants and factors.
In: Blaxter, K.L. (Ed.), Energy Metabolism. Proceedings of the

- Third Symposium. EAAP Publ. No. 11. Academic Press, London, UK, pp. 441–443.
- Choshniak, I., Ben-kohav, N., Taylor, C.R., Robertshaw, D., Barnes, R.J., Dobson, A., Belkin, V., Shkolnik, A., 1995. Metabolic adaptations for desert survival in the Bedouin goat. Am. J. Physiol. 268 (37), R1101–R1110 (Regulatory Integrative Comp. Physiol.).
- Cochran, R.C., Galyean, M.L., 1994. Measurement of in vivo forage digestion by ruminants. In: Fahey, G.C., Jr. (Ed.), Forage Quality, Evaluation, and Utilization. Am. Soc. Agron., Crop Sci. Soc. Am., Soil Sci. Soc. Am., Madison, WI, pp. 613–643.
- Drouillard, J.S., Klopfenstein, T.J., Britton, R.A., Bauer, M.L., Gramlich, S.M., Wester, T.J., Ferrell, C.L., 1991. Growth, body composition, and visceral organ mass and metabolism in lambs during and after metabolizable protein or net energy restrictions. J. Anim. Sci. 69, 3357–3375.
- Freetly, H.C., Nienaber, J.A., Brown-Brandl, T.M., 2002. Relationship between aging and nutritionally controlled growth rate on heat production of ewe lambs. J. Anim. Sci. 80, 2759–2763.
- Freetly, H.C., Nienaber, J.A., Brown-Brandl, T.M., 2003. Relationship between aging and nutritionally controlled growth rate on heat production of heifers. J. Anim. Sci. 81, 1847–1852.
- Goetsch, A.L., 1998. Splanchnic tissue energy use in ruminants that consume forage-based diets ad libitum. J. Anim. Sci. 76, 2737– 2746.
- Huston, J.E., Waldron, D.F., 1996. Comparative growth rates of Angora, Spanish, and Boer cross kids fed various diets. In: Southeast Regional Meat Goat Production Symposium. Florida A&M University, Tallahassee, FL, pp. 21–23.
- Joemat, R., Goetsch, A.L., Horn, G.W., Sahlu, T., Puchala, R., Min, B.R., Luo, J., Smuts, M., 2004. Growth of yearling meat goat doelings with changing plane of nutrition. Small Rum. Res. 52, 127–135.
- Johnson, D.E., Johnson, K.A., Baldwin, R.L., 1990. Changes in liver and gastrointestinal tract energy demands in response to physiological workload in ruminants. J. Nutr. 120, 649–655.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996.SAS System for Mixed Models. SAS Institute Inc., Cary, NC.
- Luo, J., Goetsch, A.L., Nsahlai, I.V., Johnson, Z.B., Sahlu, T., Moore, J.E., Ferrell, C.L., Galyean, M.L., Owens, F.N., 2004a. Maintenance energy requirements of goats: predictions based on observations of heat and recovered energy. Small Rum. Res. 53, 221–230.
- Luo, J., Goetsch, A.L., Sahlu, T., Nsahlai, I.V., Johnson, Z.B., Moore, J.E., Galyean, M.L., Owens, F.N., Ferrell, C.L., 2004b. Prediction of metabolizable energy requirements for maintenance and gain of preweaning, growing, and mature goats. Small Rum. Res. 53, 231–252.
- McAllister, T.A., Hristov, A.N., Beauchemin, K.A., Rode, L.M., Bedford, M.R., Partridge, G.G., 2001. Enzymes in ruminants diets. In: Bedford, M.R., Partridge, G.G. (Eds.), Enzymes in Farm Animal Nutrition. CABI Publishing, New York, NY, pp. 273–298.
- Merchen, N.R., Bourquin, L.D., 1994. Processes of digestion and factors influencing digestion of forage-based diets by ruminants. In: Fahey Jr., G.C. (Ed.), Forage Quality, Evaluation, and Utilization. Am. Soc. Agron., Crop Sci. Soc. Am., Soil Sci. Soc. Am., Madison, WI, pp. 564–612.
- Negesse, T., Merkel, R.C., Tolera, A., Goetsch, A.L., Sahlu, T., Puchala, R., Gipson, T.A., Dawson, L.J., 2001. Feed intake and growth by Spanish and Boer × Spanish doelings consuming diets with different levels of broiler litter. J. Anim. Sci. (79 (Suppl. 1)), 448.

- NRC, 1981. Nutrient Requirements of Goats. Angora, Dairy, and Meat Goats in Temperate and Tropical Countries. National Academy Press, Washington, DC, pp. 2–3.
- Nsahlai, I.V., Goetsch, A.L., Luo, J., Johnson, Z.B., Moore, J.E., Sahlu, T., Ferrell, C.L., Galyean, M.L., Owens, F.N., 2004. Metabolizable energy requirements of lactating goats. Small Rum. Res. 53, 253–273.
- Prieto, I., Goetsch, A.L., Banskalieva, V., Cameron, M., Puchala, R., Sahlu, T., Dawson, L.J., Coleman, S.W., 2000. Effects of dietary protein concentration on postweaning growth of Boer crossbred and Spanish goat wethers. J. Anim. Sci. 78, 2275–2281.
- Reid, J.T., Ottilie, D.W., Anrique, R., Fortin, A., 1980. Nutritional energetics of livestock: some present boundaries of knowledge and future research needs. J. Anim. Sci. 51, 1393–1415.
- Roeder, B.W., Ramsey, W.S., Hafley, B., Miller, R.L., Davis, E., Machen, R., 1997. Differences in growth, carcass, and sensory characteristics of young goats of different genotypes. J. Anim. Sci. 75 (Suppl. 1), 271.
- Sahlu, T., Goetsch, A.L., Luo, J., Nsahlai, I.V., Moore, J.E., Galyean, M.L., Owens, F.N., Ferrell, C.L., Johnson, Z.B., 2004. Nutrient requirements of goats: developed equations, other considerations, and future research to improve them. Small Rum. Res. 53, 191–219.
- Sainz, R.D., Bentley, B.E., 1997. Visceral organ mass and cellularity in growth-restricted and refed beef steers. J. Anim. Sci. 75, 1229–1236.
- SAS, 1998. SAS User's Guide, Version 6.12. SAS Institute Inc., Cary, NC.
- Silanikove, N., 1986. Interrelationships between feed quality, digestibility, feed consumption, and energy requirements in desert (Bedouin), and energy requirements in desert (Bedouin) and non-desert (Saanen) goats. J. Dairy Sci. 69, 2157–2162.
- Silanikove, N., 1987. Effect of imposed reduction in energy intake on resting and fasting heat production in the black Bedouin goat. Nutr. Rep. Int. 35, 725–731.
- Silanikove, N., 1992. Effects of water scarcity and hot environment on appetite and digestion in ruminants: a review. Livest. Prod. Sci. 30, 175–194.
- Silanikove, N., 2000a. Goat production under harsh environmental conditions: the physiological basis and the challenge. In: Merkel, R.C., Abebe, G., Goetsch, A.L. (Eds.), The Opportunities and Challenges for Enhancing Goat Production in East Africa. Langston University, Langston, OK, pp. 6–28.
- Silanikove, N., 2000b. The physiological basis of adaptation in goats to harsh environments. Small Rum. Res. 35, 181–194.
- Staples, C.R., Fernando, R.L., Fahey, G.C., Jr., Berger, L.L., Jaster, E.H., 1984. Effects of intake of a mixed diet by dairy steers on digestion events. J. Dairy Sci. 67, 995–1006.
- Steel, R.G.D., Torrie, J.H., 1980. Principles and Procedures of Statistics, second ed. McGraw-Hill Book Company Inc., New York, NY, pp. 401–437.
- Taylor, C.S., Young, G.B., 1968. Equilibrium weight in relation to food intake and genotype in twin cattle. Anim. Prod. 10, 393– 412
- Tovar-Luna, I. Goetsch, A.L., Puchala, R., Sahlu, T. Effects of diet quality on energy expenditure by Alpine, Angora, Boer, and Spanish wethers. Small Rum. Res., in press.
- Tyrrell, H.F., Moe, P.W., 1975. Effect of intake on digestive efficiency. J. Dairy Sci. 58, 1151–1163.
- Urge, M., Merkel, R.C., Sahlu, T., Animut, G., Goetsch, A.L., 2004.Growth performance by Alpine, Angora, Boer and Spanish wether

- goats consuming 50 or 75% concentrate diets. Small Rum. Res. 55, 149-158
- Van Soest, P.J., 1994. Microbes in the gut. In: Nutritional Ecology of the Ruminant, second ed. Cornell University Press, Ithaca, NY, pp. 281–290
- Wester, T.J., Britton, R.A., Klopfenstein, T.J., Ham, G.A., Hickok, D.T., Krehbiel, C.R., 1995. Differential effects of plane of protein
- or energy nutrition on visceral organs and hormones in lambs. J. Anim. Sci. 73, 1674-1688.
- Williams, C.B., Jenkins, T.G., 2003. A dynamic model of metabolizable energy utilization in growing and mature cattle. I. Metabolizable energy utilization for maintenance and support metabolism. J. Anim. Sci. 81, 1371–1381.